

COMPARATIVE ADAPTATIONS OF THE ALASKAN REDPOLLS TO THE ARCTIC ENVIRONMENT

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Two species (by current definition) of redpolls are involved in the present study: *Acanthis hornemanni exilipes* (Coues), the Hoary Redpoll, and *Acanthis flammea flammea* (L.), the Common Redpoll. Redpolls breed circumpolarly in arctic and subarctic regions south to approximately 54°N latitude. Populations of *hornemanni*, in general, breed farther north than those of *flammea*. Most of the North American populations are migratory to some extent, and, probably depending on the availability of food, move irregularly into the northern one-third of the United States in winter. *Hornemanni* does not move as far south as *flammea* and is considered "rare" in the United States (Audubon Field Notes, 1947-1967 Christmas counts). Some overwinter the farthest north of any small North American bird except for the Black-capped Chickadee (*Parus atricapillus*). *Hornemanni* spends at least a part of the winter at Anaktuvuk Pass, Alaska, 68°N lat. (Irving, 1960) and possibly even on the Arctic Slope of the Brooks Range, within 100 miles (69°N lat.) of the Arctic coast in Alaska (Clayton M. White, pers. comm.). Both species can be considered arctic or subarctic permanent residents. They both (*flammea* more commonly) winter fairly abundantly at Fairbanks, Alaska (65°N lat.), which although it is subarctic, receives the lowest temperature extremes of the state, occasionally down to -60 C.

Survival of so small a bird (12-14 g) at such low temperatures is remarkable and merits study. Although certain behavioral and morphological aspects in the adaptations of the species were investigated, the present study deals primarily with the gross metabolic or bioenergetic relations of the birds to their arctic environment.

The taxonomy of the redpolls is by no means resolved. According to the 1957 A.O.U. Check-list, *hornemanni* and *flammea* are regarded as distinct species, but Salomonsen (1928, 1950-51), Williamson (1961), and others believe them to be conspecific. It is well known that they commonly interbreed, and that a wide range of plumage and bill-size intergradations is found in nature. From raw data for birds from Umiat, Alaska, kindly supplied by P. H. Baldwin, calculations made indicate that in 48 birds with *hornemanni*-type plumage, bill length (\pm SD) was 7.00 ± 0.37 mm; bill depth, 5.68 ± 0.22 mm; length/depth ratio, 1.228 ± 0.03 . In 14 *flammea* types length was 7.50 ± 0.54 mm; depth, 5.61 ± 0.11 mm; length/depth ratio, 1.336 ± 0.02 . Bill length and the length/depth ratio of *hornemanni* were both significantly less than those of *flammea* and bill depth for

hornemanni was greater, but not significantly. Birds with intermediate plumage types were also intermediate in bill characters. Typical *hornemanni* specimens thus have a shorter and deeper bill than typical *flammea* specimens and in addition are much whiter and grayer (less brown), with little or no streaking on breast, abdomen, rump, and under tail coverts. Adult male *hornemanni* are also pink-breasted and rumped, whereas male *flammea* are red in these areas.

It was not the main purpose of this study to make any clear-cut decision regarding the taxonomy of these birds but the comparisons made between them may be of some use to taxonomists. Most of the birds available for research were intermediate in some morphological characteristics, but were close enough to one type or the other to be designated *hornemanni* or *flammea*.

MATERIALS AND METHODS

All redpolls were captured at two locations in Alaska and shipped to Illinois by air express. Fifteen birds from the breeding population were mist-netted during the latter half of August 1963 at Umiat, on the Arctic Slope of the Brooks Range, and 72 at Fairbanks, in central Alaska. One hundred fifty-seven birds were captured at Fairbanks at feeder traps during the latter half of March and first half of April 1964 by Heinrich K. Springer and sent in three shipments soon after capture. The birds were initially fed commercial bird seed but were gradually changed over to the experimental feed within a week. The experimental cages in which they were held measured $16 \times 30 \times 30$ cm, and have been described in detail by Martin (1967). Metal perches were wound with masking tape in the low-temperature experiments. In approximately half the cages, activity was measured as recorded on an Esterline-Angus event recorder.

The University of Illinois No. 521 chick starter feed which was used was finely ground and homogeneous, but before being given to the birds it was put through a 1.5 mm mesh screen to take out foreign and insufficiently ground particles and to facilitate subsequent separation of waste food from excreta. The feed contains approximately 4.4 kcal/g and 21 per cent protein. Grit was not given to the birds. Water was supplied at above-freezing, and snow at below-freezing temperatures.

Molt was determined by sorting and counting all loose feathers in the cage at the time of cleaning. Molt intensity values were obtained by summation, with an index value of 1 for each remex or retrix, each five body feathers or coverts, or each 15 head or neck feathers (adapted from West, 1958).

At the end of each 3-day experimental period birds were weighed on a Torsion balance to the nearest 0.01 g and were rated according to the following fat classification (modified from Weise, 1956):

- 1, no visible fat;
- 2, little fat (no fat visible between the intestinal folds, fat lining the furcula);
- 3, moderate fat (fat visible between the intestinal folds and filling the furcula);

- 4, fat (fat visible subcutaneously on the abdomen and bulging from the furcula);
- 5, very fat (fat bulging from the abdomen and furcula).

Subclasses were also recognized here, especially among the higher categories, for example, 3.00, 3.25, 3.50, 3.75, 4.00, etc.

For lipid analysis the birds were dried for 24 hours at 68 C in a vacuum oven and weighed. They were then macerated and ground in petroleum ether until the largest particles were less than 5 mm in size, and the lipid was extracted in a modified Soxhlet apparatus and weighed.

Gross energy intake was determined for individual birds during each 3-day experimental period by subtracting the weight of uneaten food from the weight of the food given and multiplying this by the caloric value of the food. *Excretory energy* was calculated by multiplying the weight of the excreta by its caloric value. Subtracting excretory energy from gross energy intake gave the *metabolized energy*. During a sequence of periods when a bird maintained constant weight (did not vary more than 0.25 g, approximately two per cent of body weight), metabolized energy was designated *existence energy*. This is defined as the energy required by a bird under caged conditions to maintain life, with only a limited number of activities such as feeding, preening, etc. Any metabolized energy above the existence level would be available for molting, reproduction, fat deposition, migration, etc. and can be termed *productive energy*.

Caloric values for food and excrement were obtained by bomb calorimetry. The samples and their weights were obtained in the following manner. Between consecutive 3-day periods each cage was cleaned and provided with fresh water or snow and a known weight of fresh food. Excreta and waste food were oven-dried together at approximately 65 C for 3 days, then separated by brushing through a 1.5 mm mesh screen (fecal pellets did not go through), and weighed to 0.01 g. An amount of food, equal in wet weight to and taken from the same supply as that given the birds, was dried and weighed at the same time to determine the dry weight of food given the birds. All samples were then stored at below-freezing temperatures until the caloric determinations were made. With the excreta these determinations were made only for periods in which the bird maintained a constant weight, and thus were presumably in energy balance.

Experiments, for which birds were always randomly chosen, were done both in controlled temperature cabinets or rooms and in an outdoor aviary protected from wind and precipitation. For all experiments (see Table 1) the birds were given previous photoperiodic and temperature conditioning, similar to the experiment, for one to three months. Examination of plumage, bill color, vocalization, and cloacal and gonadal development indicated that this conditioning period successfully put the birds in the proper phase of their annual cycle.

The cages were always cleaned and the birds weighed at the same time of day to minimize differences caused by the daily feeding cycle. Ambient temperatures were measured at 24-minute intervals with copper-constantan thermocouples placed near the birds and connected to a Leeds and Northrup recording 24-pen potentiometer. Means were calculated from all recordings in each 24-hour period. Humidity was not measured.

The outdoor experiment was run to determine whether the annual physiological cycle would be greatly altered by keeping the birds as permanent residents in Illinois. In addition, a group of birds was placed in a cabinet under a regime of simulated outdoor conditions for Fairbanks, Alaska. This group was first subjected to the daily changes in temperature and photoperiod that occurred from 2 December 1963 to 26 January 1964, and then to those from 20 November 1964 to 8 January 1965. Daily minimum, maximum,

TABLE 1
SUMMARY OF EXPERIMENTS AT DIFFERENT PHOTOPERIODS AND TEMPERATURES¹

Experiment	Time	Species ²	Sex	Initial age class	When caught
24-hour, high-temp. (32 to 38 C)	19 June-10 Aug., 1964	H	3m	3 imm.	March, 1964
24-hour, medium-temp. (9 to 11 C)	14 Aug.-4 Sept., 1964	F	7m, 2f	7 ad., 2 imm.	March, 1964
24-hour, low-temp. (-5 to -31 C)	12 Aug.-16 Nov., 1964	H	2m, 1f	3 ad.	March, 1964
		F	2m	2 ad.	
7-hour, high-temp. (31 to 39 C)	3 April-5 June, 1964	H	3m	3 ad.	March, 1964
		F	6m, 5f	9 ad., 2 imm.	
7-hour, medium-temp. (9 to 10 C)	3-29 March, 1964	H	3m	3 ad.	March, 1964
		F	2m	2 ad.	
7-hour, low-temp. (-10 to -38 C)	22 April-13 July, 1964	H	3m	1 ad., 2 imm.	March, 1964
		F	4m	3 ad., 1 imm.	
10-hour, low-temp. (-7 to -32 C)	27 Jan.-12 March, 1964	H	0	0	—
		F	3f	3 imm.	Aug., 1963
Varying-photoperiod, approx. 25 C	18 June-29 Oct., 1964	H	1m	1 ad.	
		F	5m, 2f	5 ad., 2 imm.	March, 1964
Varying-photoperiod, approx. -2 C	2 May-13 Sept., 1964	H	1m	1 imm.	
		F	6m, 1f	4 ad., 3 imm.	March, 1964
Outdoors, Illinois	10 Oct., 1963-11 Oct., 1964	H	3m, 1f	1 ad., 3 imm.	
		F	2m, 3f	3 imm., 2 juv.	Aug., 1963
Simulated Fairbanks outdoors	2 Dec., 1964-17 March, 1965	H	2m, 2f	4 ad.	April, 1964
		F	4m, 1f	5 ad.	March, 1964

¹ All birds captured at Fairbanks except the four *hornemanni* used in the outdoor experiment, which were captured at Umiat.

² H = *A. hornemanni*; F = *A. flammea*.

and mean temperatures, obtained from U.S. Weather Bureau reports, were established manually in the temperature cabinet each day for the approximate times and durations that they had occurred in Fairbanks. Photoperiods included the time from sunrise to sunset plus the percentage of civil twilight that the birds in the outdoor experiment had utilized. These percentages agreed well with data given by Franz (1943, 1949).

Daylengths (including utilized twilight) of 7 and 24 hours were considered to be most representative for redpolls during winter and summer respectively, therefore most constant-temperature experiments were run at these two photoperiods. At each photoperiod groups of birds were subjected to high temperatures (31 C to the upper limit of tolerance), medium temperatures (9 to 11 C), and low temperatures (-5 C to the lower limit of tolerance). A low-temperature experiment was also run with a 10-hour photoperiod. The birds were maintained at a constant temperature until they reached a constant weight, then the temperature was lowered or raised approximately 3 C to the next level.

A group of birds held at approximately -2 C was given a varying photoperiod schedule of 7, 3, 7, 10, 18, 24, 18, and 10 hours of light per day in that order, each period lasting

at least nine days. Another group at approximately 25 C was given a schedule of 24, 18, 10, 7, 3, and 10 hours of light. Three hours was estimated to be close to the shortest daylength encountered by redpolls wintering in central Alaska. Data for 7-, 10-, and 24-hour photoperiods at these temperatures were incorporated into the analysis of temperature effect.

After determining gross, excretory, and existence energies in the various experiments, regression lines of energy on temperature were calculated for all groups of birds. Those for the constant-temperature birds were done in the IBM 7094 computer at the University of Illinois with the help of personnel from the Statistical Service Unit.

Statistical methods used in this study were taken from Jacob and Seif (mimeo) and Steel and Torrie (1960). Unless otherwise stated, simple F tests were used in comparing values. The level of significance set for all comparisons is $P = 0.05$.

RESULTS

Redpolls under Constant Temperatures and Controlled Photoperiods

Energy relations.—The relation between gross, existence, and excretory energies is shown separately for *hornemanni* and *flammea* in Figures 1–3. In no case in Figure 3 were the slopes or any values along corresponding curves at any one photoperiod significantly different between species. The curves show a more-or-less linear increase of energy with decreasing temperature. Temperature differentials at various locations within the low-temperature cabinet, and the inability of all cabinets to hold a set temperature within 1 or 2 C for extended periods have resulted in data being used for temperatures closer together than the 3 C interval mentioned above. For this reason the curves were calculated using values for individual birds rather than means of several. Goodness-of-fit tests for the regression lines (Table 2) were significant, indicating that the lines are good representations of the numerical data.

Exponential regressions were calculated from quadratic through quintic because it seemed obvious that the data contained other than linear components. Quintic curves are shown in Figures 1 and 2 because they best fitted the points, statistically and visually. Quintic curves for 24-hour birds are not shown but they were quite similar in shape to those for 7-hour birds. Although these lines are similar in general shape, suggesting that the variations were not random, there are certain differences between them, and it is very possible that their deviations from a straight line are not actually or always of the magnitude or direction indicated in these experiments. West and Hart (1966) found a somewhat similar curvilinear relation at night but a linear relation during the daytime with the Evening Grosbeak (*Hesperiphona vespertina*). Therefore, linear regressions, representing the more general trends in the data, have mostly been used in comparing the two species of redpolls. It should be recognized, however, that the actual relation seems to be curvilinear.

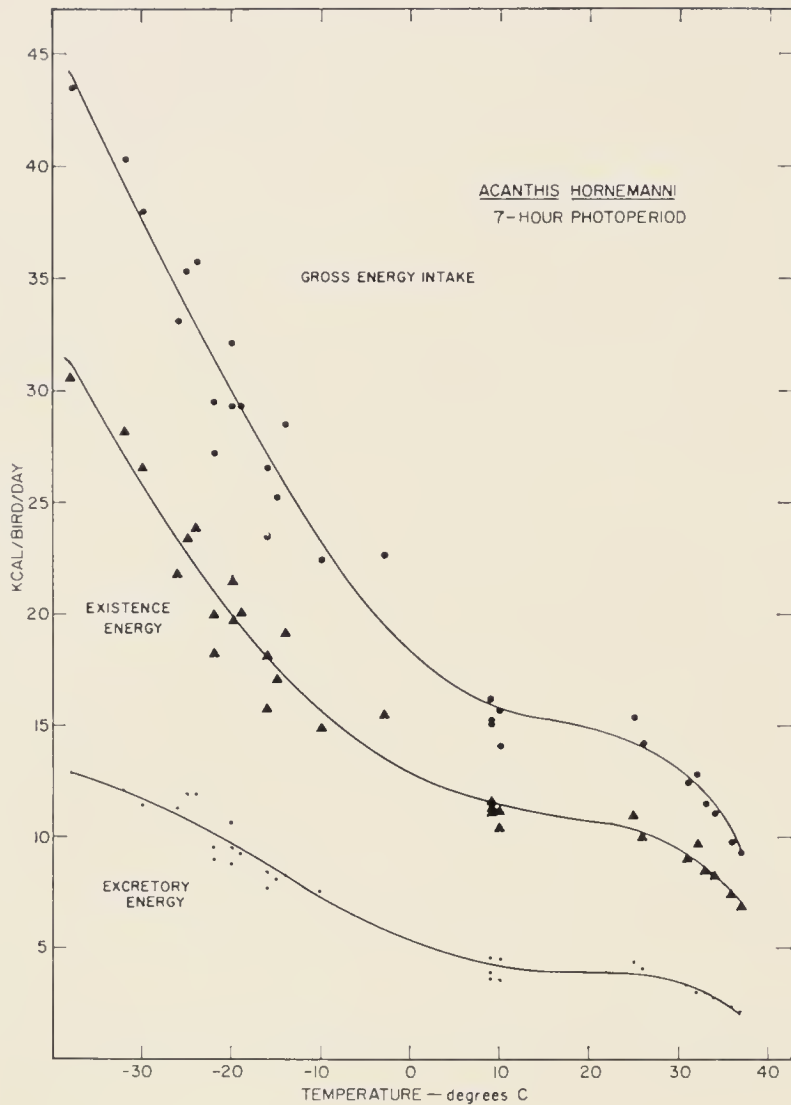


FIG. 1. Quintic regressions of energy on temperature for *A. hornemanni* at a 7-hour photoperiod.

The 24-hour gross and existence energy lines (Fig. 3) are significantly different in slope from the corresponding 7-hour lines for each species. Values on these two sets of lines for *hornemanni* are significantly different at all temperatures but for *flammea* are different only below about 20 C. Excretory energy lines are not different in any respect, although 24-hour values are somewhat higher. Values on these lines at -2 and +25 C came from the birds held at varying photoperiods.

At photoperiods of 7 hours and lower most birds at less than 0 C fed during total darkness, as did the 3-hour birds at 25 C. Seven-hour birds at extreme high temperatures also drank at night, but the amount was not determined. The amount of food consumed at night was measured at the 3-hour photoperiod, both at -2 and at +25 C. At these respective temper-

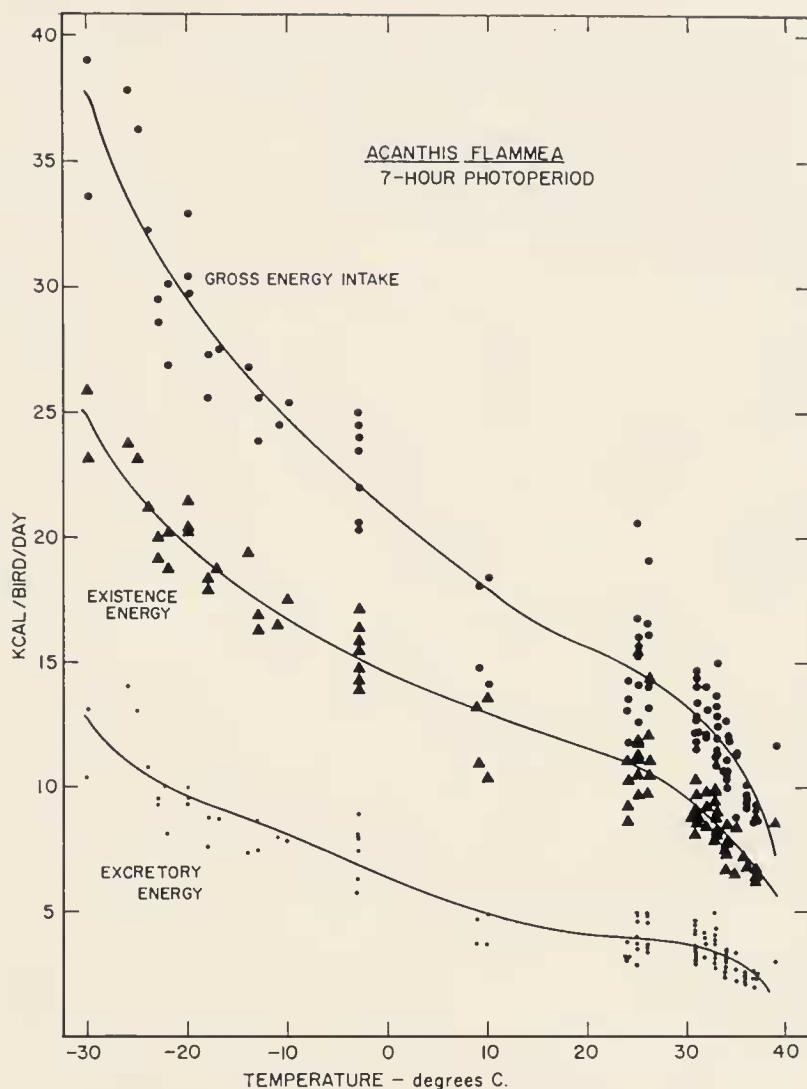


FIG. 2. Quintic regressions of energy on temperature for *A. flammea* at a 7-hour photoperiod.

atures the birds at night consumed a mean of 42 and 58 per cent of their total gross intake, although there was considerable individual variation.

The coefficient of metabolic utilization or digestive efficiency (per cent assimilated of the total calories ingested) was calculated by dividing metabolized energy by gross energy. The efficiencies shown in Figure 4 are the means calculated from constant-weight periods, and thus are comparable at any temperature or photoperiod.

Hornemanni was significantly more efficient (Chi square) than *flammea* at the extremes of temperature, otherwise the two species were essentially similar. Efficiencies increased significantly with increasing temperature at 7 hours of light but not at 24 hours. This and the fact that the 7-hour values at low temperatures were significantly lower than those at 24 hours may be

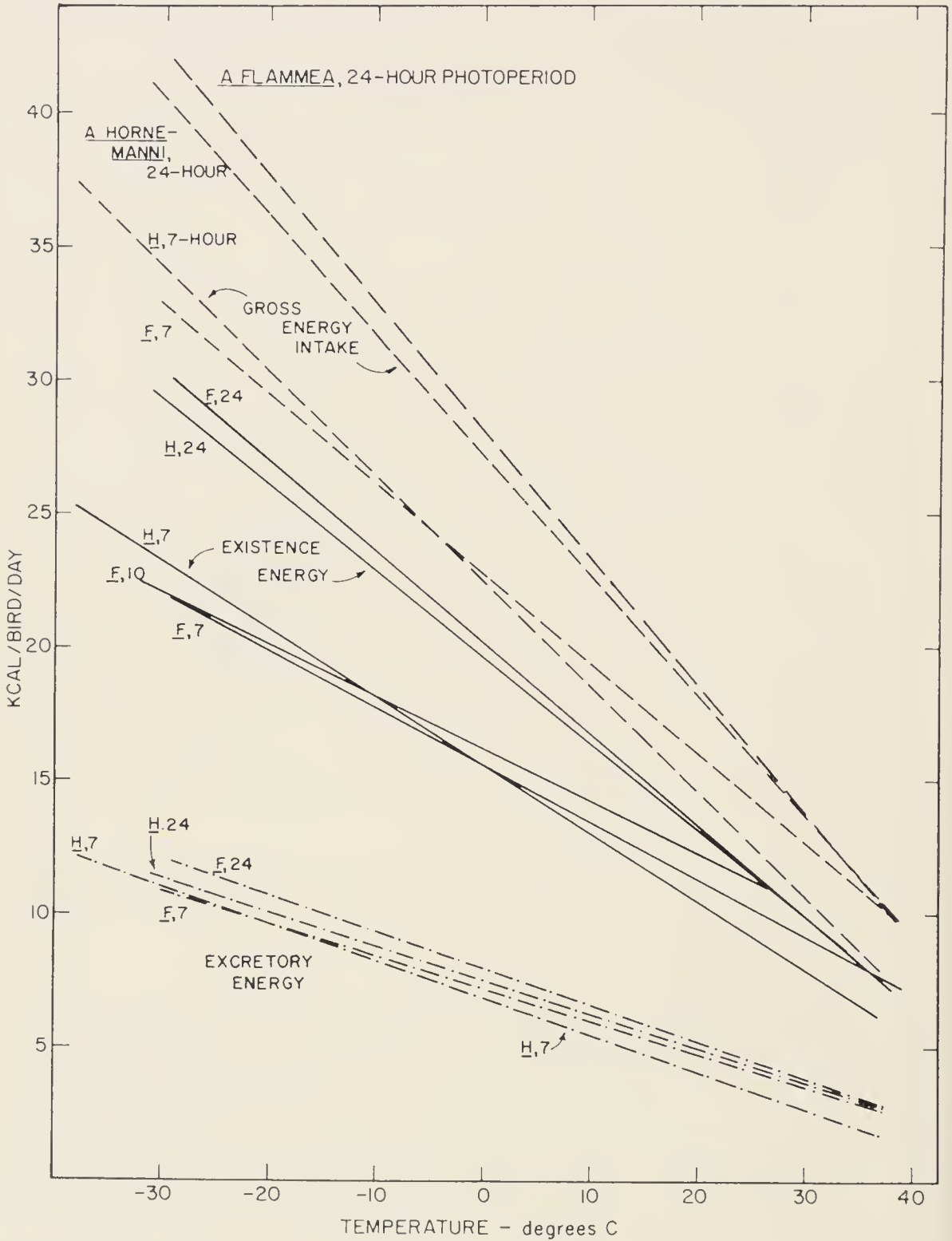


FIG. 3. Linear regressions of energy on temperature for *A. hornemanni* (H) and *A. flammea* (F) at 24- and 7-hour photoperiods. The existence energy line for *flammea* at a 10-hour photoperiod is also shown.

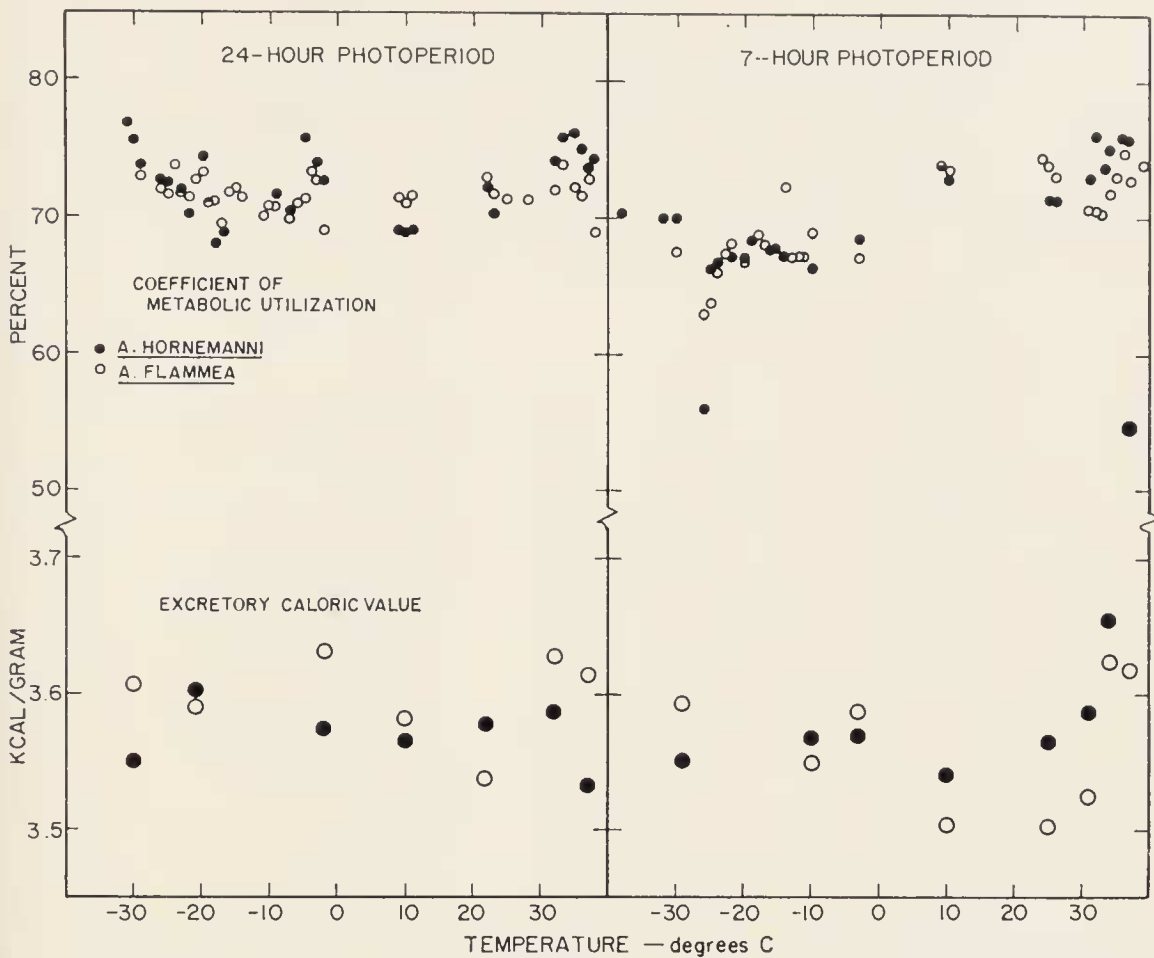


FIG. 4. Excretory caloric value and coefficient of metabolic utilization (digestive efficiency) in relation to temperature for redpolls at 24- and 7-hour photoperiods.

explained by the lower feeding rate per light hour and presumably longer retention of food in the gut of 24-hour birds. Efficiencies at high and intermediate temperatures were not different between 7- and 24-hour birds, where the feeding rates were more alike. There was also a significant increase in efficiency for *hornemanni* at temperatures of -30°C and lower at both photoperiods, but not for *flammea*. The explanation for this increase at extreme low temperatures seems to be that *hornemanni* was somehow able to retain food in the gut longer than was *flammea*, reflected in the relatively lower excretory caloric value for *hornemanni* at these temperatures (Fig. 4).

There were no significant or consistent differences in excretory caloric values between the two species or between birds at different photoperiods. However, except at high temperatures on a 24-hour photoperiod, the differences shown in efficiency are roughly inversely correlated with the caloric values per unit weight of excreta, as expected. At extreme high temperatures large amounts of fluid in the excrement made separation from waste food, with its higher caloric content, difficult and inaccurate. It should be

TABLE 2
QUINTIC AND LINEAR REGRESSION EQUATIONS OF GROSS (GE), EXCRETORY (EE), AND EXISTENCE (ExE) ENERGY ON TEMPERATURE FOR REDPOLLS UNDER CONTROLLED TEMPERATURE CONDITIONS AT DIFFERENT PHOTOPERIODS¹

	Quintic $y =$	Linear $y =$
<i>A. hornemanni</i>		
24-hour, GE	$25.217 - 0.435T + 0.0127T^2 - 0.308 \times 10^{-2}T^3 - 0.134 \times 10^{-4}T^4 + 0.370 \times 10^{-7}T^5$	$27.224 - 0.450T$
EE	$7.244 - 0.091T + 0.575 \times 10^{-2}T^2 - 0.210 \times 10^{-3}T^3 - 0.739 \times 10^{-5}T^4 + 0.256 \times 10^{-6}T^5$	$7.587 - 0.126T$
ExE	$17.973 - 0.344T + 0.697 \times 10^{-2}T^2 - 0.977 \times 10^{-3}T^3 - 0.600 \times 10^{-5}T^4 + 0.144 \times 10^{-6}T^5$	$19.637 - 0.324T$
7-hour, GE	$18.154 - 0.364T + 0.012T^2 - 0.781 \times 10^{-2}T^3 - 0.458 \times 10^{-5}T^4 - 0.461 \times 10^{-7}T^5$	$22.506 - 0.394T$
EE	$5.388 - 0.164T + 0.465 \times 10^{-2}T^2 + 0.603 \times 10^{-4}T^3 - 0.231 \times 10^{-5}T^4 - 0.338 \times 10^{-7}T^5$	$6.884 - 0.139T$
ExE	$12.766 - 0.199T + 0.750 \times 10^{-2}T^2 - 0.681 \times 10^{-4}T^3 - 0.227 \times 10^{-5}T^4 - 0.123 \times 10^{-7}T^5$	$15.621 - 0.255T$
<i>A. flammea</i>		
24-hour, GE	$26.346 - 0.548T + 0.699 \times 10^{-2}T^2 + 0.214 \times 10^{-4}T^3 - 0.545 \times 10^{-5}T^4 + 0.674 \times 10^{-7}T^5$	$28.177 - 0.477T$
EE	$7.717 - 0.158T + 0.126 \times 10^{-2}T^2 + 0.832 \times 10^{-5}T^3 - 0.149 \times 10^{-5}T^4 + 0.288 \times 10^{-7}T^5$	$7.989 - 0.136T$
ExE	$18.628 - 0.389T + 0.573 \times 10^{-2}T^2 + 0.131 \times 10^{-4}T^3 - 0.396 \times 10^{-5}T^4 + 0.385 \times 10^{-7}T^5$	$20.187 - 0.341T$
7-hour, GE	$20.910 - 0.358T + 0.324 \times 10^{-2}T^2 + 0.112 \times 10^{-3}T^3 + 0.194 \times 10^{-5}T^4 - 0.174 \times 10^{-6}T^5$	$22.804 - 0.337T$
EE	$6.405 - 0.179T + 0.258 \times 10^{-3}T^2 + 0.151 \times 10^{-3}T^3 + 0.203 \times 10^{-5}T^4 - 0.131 \times 10^{-6}T^5$	$7.211 - 0.122T$
ExE	$14.505 - 0.180T + 0.298 \times 10^{-2}T^2 - 0.388 \times 10^{-4}T^3 - 0.893 \times 10^{-7}T^4 - 0.428 \times 10^{-7}T^5$	$15.593 - 0.215T$
10-hour, ExE		$16.195 - 0.196T$

¹ T = temperature, degrees Celsius; y = energy in kcal/bird-day.

TABLE 3
LETHAL TEMPERATURES FOR INDIVIDUAL REDPOLLS¹

7-hour photoperiod		10-hour photoperiod	24-hour photoperiod	
H	F	F	H	F
37 C	37 C		38 C	35 C
	37		2 survi- vors, > 38	35
	37			37
	37			38
	37			38
	3 survi- vors, > 37			4 survi- vors, > 38
-26	-20	-32	3 survi- vors, < -33	-17
-43	-24	-32		-24
($\bar{x} = -34$)	-32	-36		-26
	-32	($\bar{x} = -33$)		-26
	($\bar{x} = -27$)			-29
				-33
				1 survi- vor, < -33

¹ Best estimates (mean or median) of limits of tolerance are in boldface for *A. hornemanni* (H) and *A. flammea* (F).

emphasized, though, that this error is cancelled out in the calculation of metabolized energy, so that the existence energy values in Figures 1-3 are not biased at any temperature on this account.

Temperature tolerance.—The temperature at which half the birds die should approximate the mean limit of tolerance for a population. Because so few *hornemanni* were available, their exact limits of tolerance could not be accurately determined in all cases (Table 3).

The lower limits of tolerance for 7- and 24-hour *hornemanni* were respectively -34 and lower than -33 C, and for *flammea*, -27 and -26 C. This did not support the expectation that birds with only 7 hours of light would not withstand lower temperatures than birds with constant light. The insulative value of the plumage was probably decreased in summer-plumaged (24-hour) birds due to an apparently normal loss of fair numbers of body feathers which was observed. White (pers. comm.) has found that wild birds had a 31 per cent heavier plumage in November than in July. The increase in caloric intake (Fig. 3) was apparently almost completely offset

TABLE 4
LIVE BODY WEIGHT AND FAT CLASS OF REDPOLLS AT CONSTANT TEMPERATURES¹

Photo-period	Temp. (C)	N		Body weight (grams) ²		Fat class	
		H	F	H	F	H	F
7 hours	-38	1	-	17.41	-	3.0	-
	-32	1	1	17.12	13.57	3.0	1.8
	-29	2	2	16.56 ± 0.32	15.22 ± 0.66	3.1	2.9
	-25	2	3	16.26 ± 0.24	15.07 ± 0.39	3.0	2.6
	-21	3	4	15.65 ± 0.76	15.02 ± 0.40	2.9	2.9
	-15	3	4	15.42 ± 0.60	15.50 ± 0.14	3.2	3.5
	-10	3	4	15.20 ± 0.66	15.52 ± 0.40	2.9	3.3
	- 2	1	7	15.57	15.53 ± 0.46	3.0	3.6
	10	3	2	13.78 ± 0.42	16.10 ± 1.33	3.5	4.4
	25	1	7	13.05	14.93 ± 0.44	2.9	4.3
	31	1	11	13.33	14.34 ± 0.42	2.8	4.0
	33	1	11	13.18	14.18 ± 0.45	2.9	4.0
	34	1	11	12.88	13.71 ± 0.43	2.9	3.8
	37	1	10	10.93	12.31 ± 0.25	2.4	3.3
24 hours	-31	3	3	15.39 ± 0.43	15.50 ± 0.19	3.9	3.3
	-25	3	6	15.45 ± 0.34	15.38 ± 0.53	3.7	3.6
	-21	3	6	14.98 ± 0.35	15.46 ± 0.53	3.6	3.6
	-17	3	6	14.41 ± 0.34	15.56 ± 0.46	3.3	3.8
	- 5	3	7	14.03 ± 0.47	15.51 ± 0.44	3.3	4.0
	- 2	1	7	15.92	15.65 ± 0.18	4.6	4.8
	10	3	2	13.89 ± 0.73	15.39 ± 1.83	4.2	4.3
	25	1	7	12.71	14.06 ± 0.41	4.2	4.1
	32	3	9	14.03 ± 0.24	14.48 ± 0.31	4.5	4.5
	35	3	9	13.24 ± 0.18	13.51 ± 0.31	4.3	4.3
	37	3	7	11.97 ± 0.59	12.65 ± 0.42	3.8	4.0
	38	2	6	12.21 ± 0.65	11.96 ± 0.37	3.8	3.9
10 hours	-32	-	3	—	14.08 ± 0.15	-	2.9
	-26	-	3	—	14.69 ± 0.42	-	3.2
	-20	-	3	—	14.78 ± 0.52	-	3.3
	- 7	-	3	—	14.75 ± 0.63	-	3.4
	- 2	-	7	—	15.92 ± 0.32	-	4.2
	25	-	7	—	15.36 ± 0.82	-	4.6

¹ Different groups of birds were used at low, intermediate, and high temperatures, as indicated by the spacing. H = *A. hornemanni*, F = *A. flammea*.

² Means ± SE.

by the increased heat loss and by energy expenditure for the greater amount of locomotor activity (Fig. 5). The lower limit for 10-hour (winter-plumaged) *flammea* was -33 C, significantly lower than for 7-hour birds.

This was to be expected, since the former had more time available for intensive feeding and for maintenance of insulation (preening).

The upper limits for 7- and 24-hour birds were respectively 37 C and probably 38 C or greater. This difference may be significant. The 24-hour birds not only had reduced plumage but, probably of most importance, were able to see and to drink freely at all times, and thereby were able to withstand a slightly higher temperature.

Activity.—Activity data (Fig. 5) were combined for all birds because no significant differences could be distinguished between the species. Changes in total activity at different temperatures were very similar at both 7- and 24-hour photoperiods, with a peak between 25 and 30 C, a sharp decrease above 30 C, a more gradual decrease from 30 to -20 C, then a small increase to about -30 C. Inactivity at low temperature conserves energy and heat loss is retarded. At very high temperatures, on the other hand, inactivity reduces the amount of heat that must be lost from the body.

Body weight and fat class.—Females and males were of equal weight. In general, decreasing temperatures were correlated with increasing weight (Table 4). However, separate groups of birds were used at the intermediate temperatures and their weights do not fall exactly into place in the table. In the low-temperature experiments at both 7- and 24-hour photoperiods, *hornemanni* increased significantly in weight but *flammea* remained about the same. At the end of the 7-hour experiment *hornemanni* had become significantly heavier than *flammea*, and at the 24-hour photoperiod, had equalled *flammea* in weight, whereas it had been significantly lower at the beginning. In the 7-hour low-temperature experiment (-10 to -38 C) *hornemanni* did not change appreciably in fat class with a drop in temperature, but at 24 hours (-5 to -31 C) it increased significantly (Chi square), and in both cases its fat class at the end of the experiment was significantly higher than that of *flammea*. *Flammea* decreased significantly in fat class at both photoperiods. Both species decreased significantly in weight and fat class at temperatures above 31 C.

Outdoor Redpolls

Energy relations.—Linear regression lines of existence energy on temperature for *hornemanni* and *flammea*, using mean values obtained during constant-weight periods at various temperatures within the range of -15 to +30 C, are fitted respectively by $y = 16.920 - 0.223T$, and $y = 16.878 - 0.237T$, where y is existence energy in kcal/bird-day and T is the Celsius temperature. The mean photoperiod for these birds was about 13 hours. The lines for the two species were not significantly different. Values for all months, except September and October 1964, did not deviate significantly

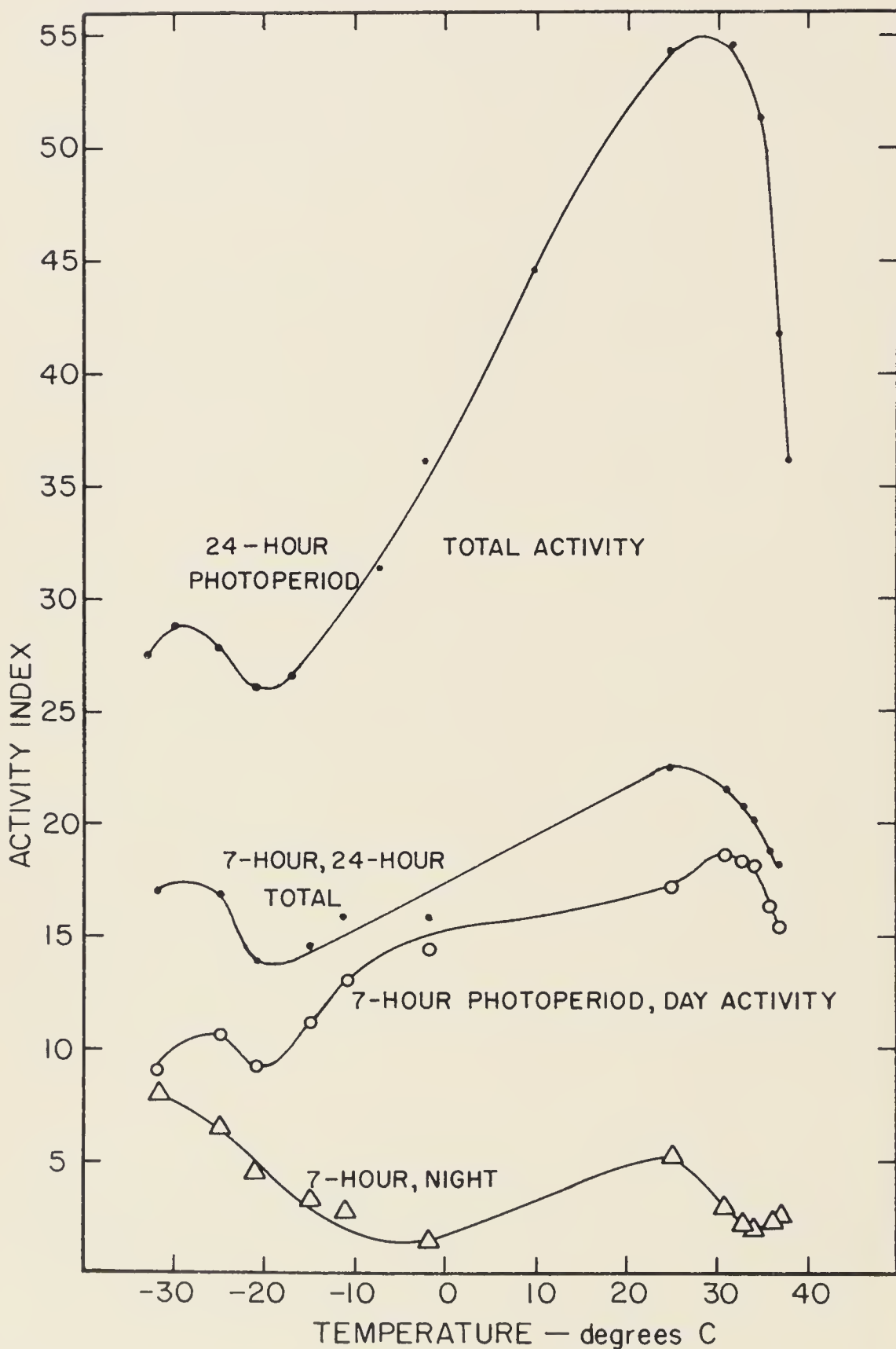


FIG. 5. Combined recorded cage activity at various temperatures. One activity index unit equals approximately 15 minutes of activity. Lines drawn by eye.

from these lines. Values for these two months, however, were significantly lower (1.5 and 2 kcal, respectively), apparently as a result of increased insulation due to the completion of molting. It appears that in the entire range of about 7 to 24 C ambient temperature there was a uniform saving of about 2 kcal/bird-day (13–17 per cent) due to having molted.

The exceedingly high productive energy values obtained during the first half of October 1963, shown in Figure 6, are not reliable because the technique of separating waste food from excreta had not yet been perfected and excrement was lost due to over-vigorous screening. Otherwise, peaks of productive energy were well correlated with temperature, fat deposition, and molt. It is evident that peaks and lows of productive energy were exactly synchronized between the two species when energy was only temperature dependent (December), but that synchrony was less perfect at other times, when this energy was correlated with fat deposition or molt. The total productive energy for the year was higher for *hornemanni*, but not significantly.

Metabolic efficiency was almost always about one per cent higher for *hornemanni*, but the differences between species were never significant. Fluctuations in efficiency were small in both species.

Activity.—Diurnal activity indices (Fig. 6) were essentially identical for *hornemanni* and *flammea*. Nocturnal activity, however, was somewhat different. Peaks of nocturnal unrest came slightly, but probably not significantly, earlier in spring and later in autumn for *hornemanni* and this species exhibited a higher intensity than *flammea*.

The hourly pattern of diurnal activity was bimodal throughout the year: higher values from just after awakening to midmorning, lower values in early afternoon, and higher values again just before activity ended. Differences between the highs and lows were of greater magnitude in summer, indicating that a more constant volume of activity per hour was maintained in the colder months. Nocturnal activity (*Zugunruhe*) in autumn was spread throughout the night but diminished somewhat in the hours around midnight. Spring *Zugunruhe*, however, was concentrated in the hours after midnight, perhaps indicating that redpolls are more often night migrants in autumn. Palmgren (1936) reports night migration of redpolls in autumn, and I infer from his paper that it is uncommon in arctic finches.

The duration of diurnal activity was generally somewhat greater for *hornemanni* than for *flammea* (Fig. 6). The difference can be attributed to greater utilization of civil twilight (earlier arising and later retirement) by *hornemanni*, to the extent that it was active an average 6 minutes per day longer than *flammea* for the year.

Body weight and fat class.—The mean bimonthly changes in weight and fat class were generally well correlated with each other (Fig. 6). However,

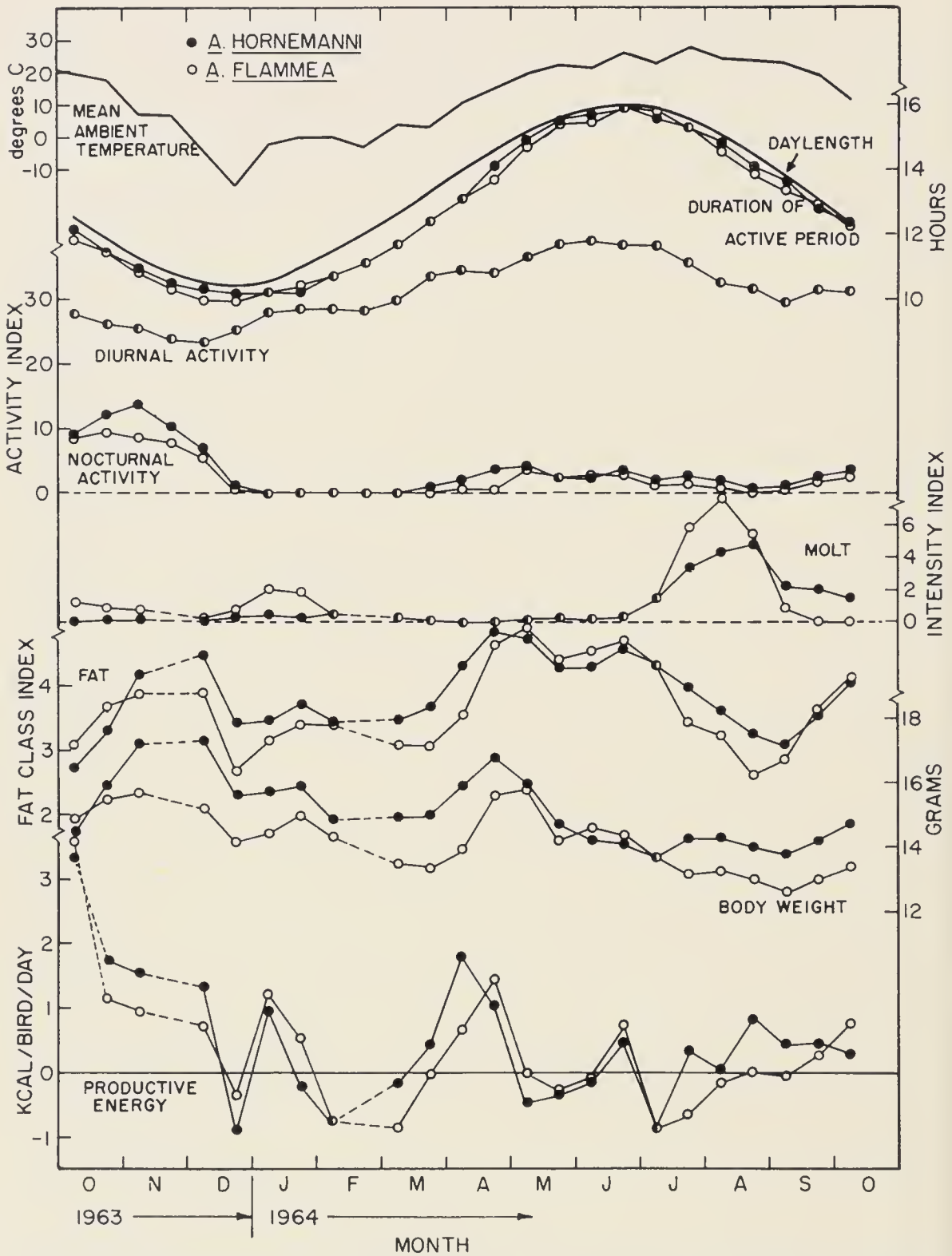


FIG. 6. The annual cycles of *A. hornemanni* and *A. flammea* held outdoors in Illinois. Values are bimonthly means. Daylength includes civil twilight.

the birds were of equal or lower weight in October 1964, yet had a higher fat class than in October 1963. This might be explained by the birds having relatively more muscle, with its higher specific gravity, than fat at

the beginning of the experiment. Caging obviously causes a significant reduction in flying, and there may be atrophy of the pectoral musculature.

Changes in fat class were closely synchronized between the species only in December and January, when they were influenced by temperature alone. The other peaks and lows were associated with migration and molt, and were not as exactly synchronized between species, but the differences were probably not significant. In general *hornemanni* was significantly heavier than *flammea* and had a higher fat class (not significant), but at certain times of the year there was no difference in weight (October 1963 and May to July 1964).

Molt.—The peak of postnuptial molt was reached later in *hornemanni* than in *flammea*, was more prolonged, and of lower intensity (Fig. 6). Molt extended over a period of 114 days for *hornemanni* but only about 65 days for *flammea*, each as a group. The mean length for individual birds was 80 days for *hornemanni* and 61 days for *flammea*. The sequence of feather loss in their molts was similar and apparently normal with respect to wild birds.

*Redpolls under Simulated Fairbanks, Alaska, Temperature,
and Photoperiod Conditions*

Energy relations.—Existence energy was calculated from periods when the birds maintained constant weight. Regression equations for existence energy on temperature within the range of -45 to -7 C, were for *hornemanni* and *flammea* respectively, $y = 15.575 - 0.308T$ and $y = 15.079 - 0.314T$. They were essentially similar both in means and slopes. When plotted, the points appear to merge with the points obtained for the outdoor birds between -15 and -7 C (Brooks, 1965), and the curvilinear relation suggested by the points for the birds held at constant temperatures (Figs. 1 and 2) again becomes apparent. No combined regression lines were computed, however.

Temperature tolerance.—Although these birds under fluctuating conditions were at a shorter photoperiod, their low-temperature tolerance was greater than that of those under constant conditions. The lethal temperatures for individual birds, calculated as the mean temperature for a period of 3 days prior to death, were, for individuals of *hornemanni*, -42 , -44 , -44 , and -45 C, and for individuals of *flammea*, -21 , -33 , -34 , -35 , and -41 C. The italicized values are median estimates of the lower limit of temperature tolerance. *Hornemanni* was better able to withstand low temperatures, except for one *flammea* individual which lived through all the "cold spells" that were lethal to *hornemanni*, but died at a higher temperature almost one month later. This bird was noticeably less excited by handling than any other bird in

all the experiments and may have been able to withstand lower temperatures because it was less stressed by caging and handling.

General

The weight of total body lipids was not directly proportional to fat class but rather was related curvilinearly (Fig. 7). The curve is fitted by the equation: $y = 1.3235 - 0.256x + 0.1451x^2 - 0.301x^3 + 0.1147e^x$, where y is grams of total lipids and x is fat class. The difference in weight of lipids between classes 1 and 4 was only about 1.0 g, while the difference between 4 and 5 was about 2.5 g. The fat classes can be used to estimate roughly the total lipids of a bird by using the values on this curve.

It became apparent during the experiments that the head and body feathers of *hornemanni* were longer and fluffier than those of *flammea*, but no size measurements were made. However, the dry weights of the plumage of 7 *hornemanni* and 7 *flammea*, randomly chosen from winter-plumaged birds which died soon after capture, gave the following results (means \pm SD):

hornemanni; total plumage, 1.0258 ± 0.10 g; head and body, 0.8386 ± 0.09 g; flight (remiges and rectrices), 0.1871 ± 0.03 g.

flammea; total plumage, 0.9506 ± 0.08 g; head and body, 0.7472 ± 0.05 g; flight, 0.2034 ± 0.03 g.

Only head and body plumage weights were significantly different between the two species, with *hornemanni* having the heavier plumage, and consequently, a better body insulation. The *hornemanni* and *flammea* specimens used here had respective mean fresh body weights of 13.22 and 13.58 g (not significantly different), indicating that the differences in weights of feathers were not due to size differences of the birds.

DISCUSSION AND CONCLUSIONS

Redpolls under Constant Temperatures and Photoperiods

Birds at low temperatures.—As expected, *hornemanni*, and to a lesser extent, *flammea*, tolerated lower temperatures than any passerine yet investigated at the University of Illinois, from tropical permanent residents to arctic summer residents (Cox, 1961; Zimmerman, 1965*b*; Olson, 1965; Kendeigh, 1949; Davis, 1955; West, 1960).

Heat production and retention are the major problems of birds at low temperatures. The main source of heat production is shivering, according to West (1962) who worked with redpolls and Evening Grosbeaks. By increasing energy intake, not only is more energy available for shivering, but specific dynamic action (SDA) also increases and contributes to the total heat production. In the present study and in those by Kontogiannis (1965), Olson (1965), Williams (1965), and Zimmerman (1965*a*) an

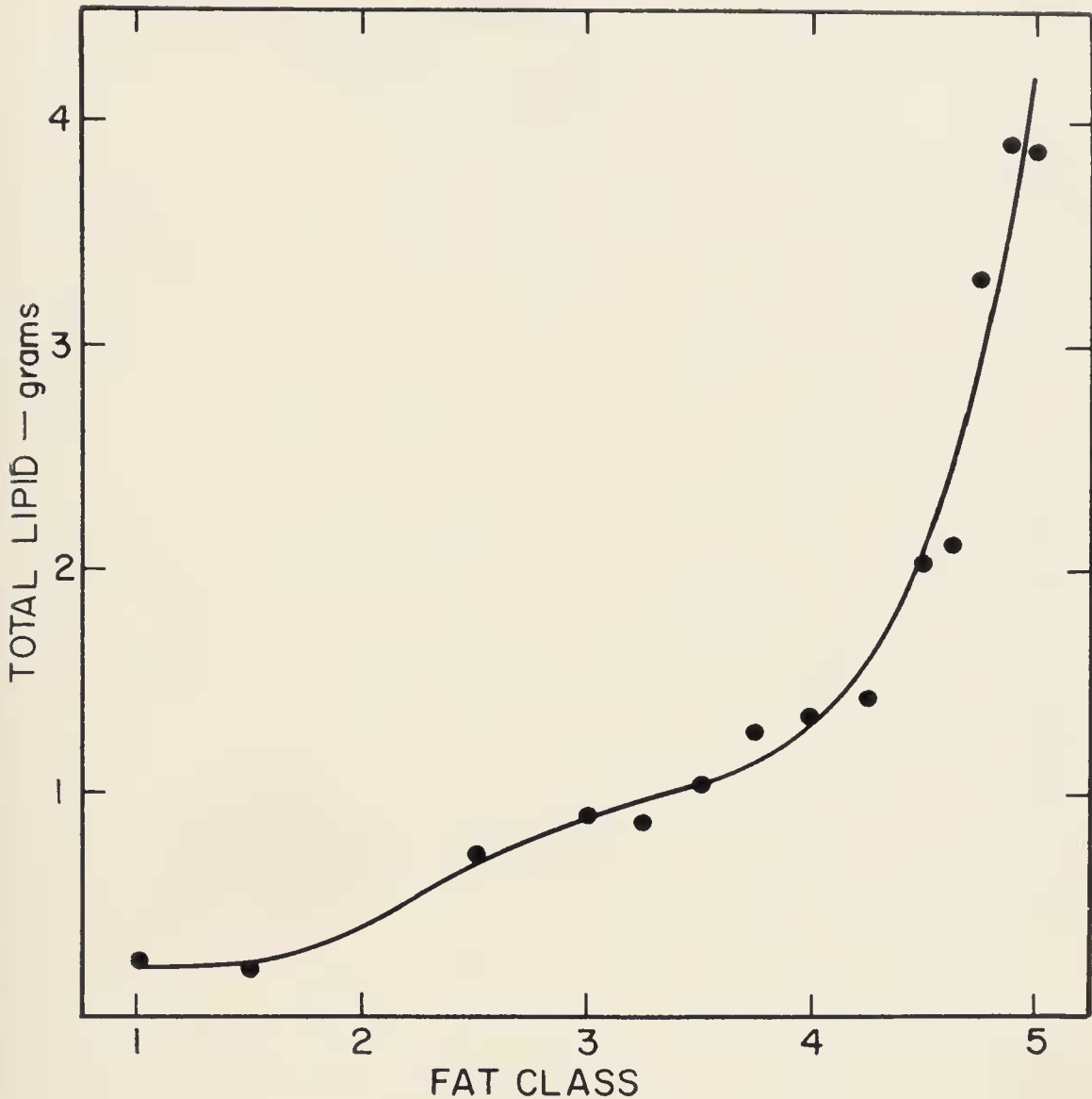


FIG. 7. Relation of total body lipids (dry weight) to fat class of redpolls.

increase in lean dry weight or protein with decreasing temperatures below about 0 C was shown (redpoll data given in thesis, Brooks, 1965). The increase in muscle mass (protein) and shivering are probably interrelated.

Retention of heat is facilitated by fluffing the feathers, by becoming inactive, by seeking shelter, and according to West (1962), by peripheral vasoconstriction. Reduction of locomotor activity, shown rather well in this study (Fig. 5), was necessary for obtaining maximum insulation from the fluffed-out plumage of the redpolls.

The most beneficial shelter would probably be a cavity of some sort, since there is a considerable saving of energy in these circumstances (Kendeigh, 1961). The dense foliage of white spruce (*Picea glauca*), which redpolls often utilize at Fairbanks, is almost as good as a cavity. in that the birds are not

radiating to the night sky. Cade (1953) has reported redpolls entering and feeding in holes in the snow formed either by protruding vegetation or by the birds themselves, and Irving (1960) writes that Eskimos at Anaktuvuk Pass have also seen this behavior. Whether it is primarily to obtain shelter or food is not known, nor is the extent to which it is done. I have observed redpolls held in flight cages in Illinois burrowing through piled snow given to them for drinking purposes, but their actions indicated that they were bathing or dusting rather than finding shelter or food.

The breeding distribution of *flammea* is very well correlated, according to Peiponen (1962), with the distribution of dwarf birch (*Betula nana*, *B. tortuosa*, and others). Having been snow-covered through the winter, seeds of these small "trees" are readily available in the spring when the seeds of larger trees have been blown away. He also found that these birds are "largely specialized" in feeding. Birch seeds, when available, make up over 80 per cent of the diet in northern Finland, even for young birds in the nest. Indeed, the German common name for this species is "*Birkenzeisig*," literally, "birch siskin." White (MS) determined that for redpolls in the vicinity of Fairbanks the proportion of birch and alder (*Alnus*) seeds in the diet was 88 per cent.

From the linear regression equations in Table 2 it can be calculated that gross energy intake at the lower limit of temperature tolerance in the 7-hour experiments was 35.9 kcal/bird-day for *hornemanni* and 31.9 for *flammea*. On the experimental diet having a caloric value of 4.4 kcal/g, the corresponding weights of food ingested would be respectively 8.2 and 7.3 g. The caloric value of unhusked birch seeds, however, is about 5.5 kcal/g (White, MS). Assuming the same metabolic efficiency, substitution in the regression equations indicates that weights of birch seeds equal to the weights of experimental feed ingested would permit tolerance of temperatures to about -57°C by *hornemanni*, and to about -51°C by *flammea*. If, rather than using calculated weights (from the regression equations), the actual weights of feed ingested by the birds (these values were somewhat higher) are used in this computation, it is found that the extrapolated lower limit of temperature tolerance is then somewhat lower than -62°C for both species. These values are all fairly close to the lowest temperatures that wild redpolls are subjected to near Fairbanks (-57°C :Johnson, 1957; -60°C :Pewe, 1964). It should be kept in mind that these are average limits for the redpoll population, and that about half the population can be expected to withstand considerably lower temperatures. The seeds of birch are substantially higher in caloric value than most types which have been measured (Kendeigh and West, 1965; Turček, 1959), thus the adaptive value of the redpolls' selectivity of birch seeds in the wild is self-evident.

The esophageal diverticulum of the redpolls, absent in most fringillids but present in several northern forms (e.g., crossbills, *Loxia* spp.), is a partially bilobed ventro-lateral outpocketing located approximately halfway between head and body (Fisher and Dater, 1961). White (MS) has found this structure to contain a maximum of 1.3 g of birch seeds in wild birds, or about 7 kcal of energy. Without this "extra" food resource the extrapolated lower limit of temperature tolerance for *hornemanni* would be reduced to about -40 C, and for *flammea*, to about -30 C. In the present study the birds at low temperatures were observed to fill their "crop" just prior to the lights going off.

Feeding in total darkness by the experimental birds at low temperatures probably depended on their having a ready food source and knowing exactly where it was. Johnson (1957) and Heinrich Springer (pers. comm.) never observed feeding during the dark near Fairbanks, although Brina Kessel (pers. comm.), at the same location, reports that during the winter redpolls were active earlier in the morning than other birds, when, to her eyes, it was still dark. Palmgren (1936) noted that redpolls caged indoors were different from other small birds in being active even under very dim light conditions. Palmgren also mentions that redpolls have been heard in migration at night, and outdoor birds in the present study showed *Zugunruhe*, but, of course, this activity is far different from searching for and feeding on small seeds. The Gray Jay (*Perisoreus canadensis*) manufactures and caches pellets of food for later consumption (Dow, 1965), and it would seem to be very advantageous for a bird like the redpoll, which can be active during darkness, if it were to cache food in or near its roosting place. However, redpolls are not known to do this. Perhaps the advantage in being able to be mobile at very low light intensities is that in the morning redpolls can fly out to the feeding area in near-darkness and be ready to feed as soon as light is sufficient to see the small seeds. In the evening they can remain at their feeding until the last light, and then make their way back to the roost again in near-darkness. Such a capability would extend considerably their actual feeding period in the long Alaskan twilight. Further observations of wild birds are required on the question of nighttime feeding before it can be stated definitely that its occurrence was a laboratory artifact, since redpolls are suspected of wintering above the Arctic Circle where there are no daylight hours during the winter.

Concerning body insulation, in addition to the "normal" body plumage, redpolls have numerous down-feathers in the apterylae during the winter, unlike a large number of other small birds. Irving (1960) ranked 12 species of fringillids in order of the "apparent usefulness for insulation" of their

contour feathers. Only the Pine Grosbeak (*Pinicola enucleator*) was higher, *hornemanni* and *flammea* ranking second and third respectively. His criteria for better insulation were, feathers "having less rigid terminal barbs with softer barbules containing extended fine processes." Retention of air within the plumage is presumably greater with these feathers. The apparent greater fluffiness of the body feathers of *hornemanni*, and the demonstration that the dry weight of the winter plumage on the head and body of *hornemanni* was significantly greater than that of *flammea*, have already been mentioned, both facts pointing to the correctness of Irving's ranking of these species.

At 7 hours of light *hornemanni* exhibited a higher rate and capacity of energy intake below 0 C than *flammea* (Fig. 3). It gained weight and did not decrease in fat class with temperatures decreasing below -5 C, while *flammea* did not gain weight and its fat class decreased. *Hornemanni* presumably, then, was able to spend more time with activities such as preening, which is, of course, very important in maintenance of insulative value of the plumage.

Steen (1958) has suggested that small arctic birds in the wild, including redpolls, undergo marked hypothermia at night at low ambient temperatures. He was able to show this only in newly caught birds, not in birds that had adjusted to caging. West (1962) suggests that these newly caught birds were subnormal. Redpolls, studied by West, that dropped more than 4 degrees in body temperature during their first nights after capture "lost weight or ultimately did not survive." There was no evidence that birds were hypothermic at any time in the present study. If it were true, one would expect to see a leveling off or a dip in the low-temperature regions of the curves in Figures 1 and 2. There is indeed the hint of a leveling off at the extreme low temperatures in all curves but this is at or beyond the lethal point for most of the birds, and since the birds here were rapidly becoming moribund, they would be expected to be subnormal.

Birds at high temperatures.—The problems here, in direct contrast to those at low temperatures, are in reducing heat production and increasing the rate of heat loss from the body. Redpolls employed the only two major methods of reducing heat production, the most important being a reduction in activity (Fig. 5), since most of the body heat is produced by muscular contraction. They also consumed less food, thus reducing the heat from SDA.

Evaporation of water from respiratory surfaces in birds is of major importance for heat dissipation as long as water is available. It has already been mentioned that redpolls drank copious amounts of water at high temperatures, no doubt for this purpose. Reduction in the insulative value of the plumage by wear or loss of feathers, and sleeking down the feathers to decrease the thickness of insulation and expel trapped warm air were also

methods employed by redpolls. Birds in winter plumage (7-hour photoperiod), when subjected to the high-temperature regime, were observed to pluck out body contour and down-feathers. Birds in summer plumage (24-hour photoperiod) had already reduced their plumage in the normal spring feather loss, and started their postnuptial molt during the experiment. Nevertheless, self-plucking was observed here, also. This plucking out of feathers may be an adaptation to the relatively rare occurrence of high temperatures in the arctic, when they must quickly reduce their insulation. Since the time of year when high temperatures occur is shortly before the birds' normal molt, the period of reduced insulation against cold would not last long.

The upper limit of temperature tolerance for *flammea* is lower than that for other passerines similarly studied, and may also be lower for *hornemanni*, although this was not determined exactly. For central Alaska the highest recorded temperature is 37.8 C (Pewe, 1964), almost exactly the same as the upper limit of temperature tolerance determined for redpolls.

Redpolls under Outdoor Fluctuating Temperatures and Photoperiods

The composition of the Umiat redpoll population is a matter for debate, some workers (Bee, 1958) referring all birds to *flammea*, some (Baldwin, 1955) to *hornemanni*, and others (White, pers. comm.) to both species plus intergrades. The outdoor birds used in this study from Umiat were rather typical *hornemanni* and those from Fairbanks, typical *flammea*. For convenience they have been referred to as these species in the present study, but it may be more correct to regard them simply as representing two different breeding populations of *Acanthis* from northern and from central Alaska.

Hornemanni, representing the northern population, showed *Zugunruhe* and reached a peak in this and fat deposition slightly earlier in spring and somewhat later in autumn than *flammea* (Fig. 6). This is a common relation in migration between northern and southern populations among other species (Lincoln, 1950). Fat deposition times of the outdoor birds correspond fairly well with those given by White (MS) for Fairbanks and for northern Russia by Blyumental (1961). Blyumental has also shown that postnuptial molt, autumn fat deposition, and migration overlapped in arctic *flammea* as they did for the other arctic species she studied. There was little overlap in the present study for *flammea* (subarctic) but considerable overlap for *hornemanni* (arctic).

The postnuptial molt in *hornemanni* began slightly later and reached a peak considerably later than in *flammea* (Fig. 6). The time of beginning molt for *hornemanni* coincides with that in wild birds at Umiat, but the duration of 80 days was approximately twice as long as in wild birds

(Baldwin, 1955). Possibly this was due to the stress of caging and handling, and perhaps the more rapid decline of photoperiod at Umiat, compared with Illinois, was also involved.

Productive energy for *flammea* increased during the molt but the birds were still in negative energy balance. However, they lost considerable fat during this time, indicating that this was a supplementary energy source. By using 9.5 kcal as a rough estimate of the energy gained from one gram of dry fat, and estimating, from Figure 7, the grams (dry weight) of fat used, the deficits of July and August are accounted for.

It is of interest that during the molt *hornemanni* continued to meet most of its energy needs by feeding and did not reduce its body fat reserves as much as did *flammea*. This behavior may have definite survival value in the far north where it is colder in summer and more subject to early and sudden periods of cold.

Regression lines for existence energy of outdoor birds paralleled but were higher than those for birds at constant temperatures and a 7-hour photoperiod. These higher mean daily values for the outdoor birds were due to the longer photoperiods (averaging 13 hours), because the birds' hourly values were lower than those of the constant-temperature birds, although not significantly. The slopes and means for the simulated Fairbanks "outdoor" birds' existence energy lines, however, were significantly steeper and higher (except at temperatures near 0 C) than those of the 7-hour birds, even though the simulated birds were exposed to shorter photoperiods (averaging 6 hours). West and Hart (1966) determined that the metabolism of Evening Grosbeaks was not significantly different under either constant or fluctuating temperature conditions in the range of about -10 to +20 C, although the values for fluctuating conditions were somewhat higher throughout. This was contrary to the findings of others, and their explanation was that in both cases the birds had been either acclimated or acclimatized to the respective conditions, whereas they had not in other studies. In the present study the redpolls were also acclimated to constant conditions or acclimatized to fluctuating conditions. It therefore appears that in these considerably smaller birds with their higher intrinsic metabolic and heat-loss rates, low fluctuating temperatures are correlated with relatively higher metabolism than are low constant temperatures, but at less severe temperatures the relation is similar to that in the grosbeaks. If this is the case, the low-temperature metabolic rates and lower limits of tolerance determined for the simulated birds in the present study are probably more indicative of those of birds under natural conditions than are those of the low-temperature 7-hour birds. At temperatures above -10 C or so this does not hold, and here the constant-temperature birds' values are as good as any.

Assuming this interpretation to be correct, substitution (into the respective regression equations) of the caloric value of birch seeds and the weight of feed ingested at the lower limit of temperature tolerance, as was done earlier with the constant-temperature birds, indicates that the estimated lower limit of tolerance in the wild for *hornemanni* would be about -67 C, and for *flammea*, about -54 C (using the simulated birds' values). These figures, in relation to the absolute Fairbanks minimum of -60 C indicated earlier, show better agreement than do those of the constant-temperature birds.

In the outdoor experiments *hornemanni* averaged 6 minutes per day greater utilization of civil twilight throughout the year than *flammea*. The bimonthly mean difference varied considerably but *hornemanni* was generally active at lower light intensities. This may be another adaptive difference between the two species. Since civil twilight lasts about four times as long in central Alaska as in Illinois, *hornemanni* should average from 20 minutes to one-half hour longer activity than *flammea* each day there. This, however, needs corroboration from studies on the wild population.

A brief comment on the taxonomic status of the redpolls may be in order at this concluding point. In the present study *hornemanni* has been shown to be better adapted to the arctic environment than *flammea*, particularly by its significantly greater tolerance of low temperature, attributable to the cumulative effects of several small and often nonsignificant differences. Apparently, due to interbreeding between *hornemanni* and *flammea*, a complete gradient of morphological types occurs. It would not seem unreasonable to assume that a physiological gradient exists as well, with typical specimens of *hornemanni* and *flammea* occupying different positions on it. In view of this and the fact that natural interbreeding occurs, the only logical answer seems to be that there is but one species of *Acanthis* here, *hornemanni* and *flammea* being, at best, subspecies adapted to slightly different environments.

SUMMARY

Inverse linear as well as curvilinear correlations of metabolized energy (kcal/bird-day) with temperature were demonstrated under both constant and fluctuating temperatures between -30 and $+38$ C for *Acanthis hornemanni exilipes* (Hoary Redpoll) and *A. flammea flammea* (Common Redpoll) at winter and summer photoperiods. Digestive efficiency generally decreased initially with a drop in temperature but increased after a long duration at low temperature, especially at extreme low temperatures, and particularly with *hornemanni*.

The lower and upper limits of temperature tolerance determined for birds held at constant temperatures were respectively: *hornemanni*, -34 to $+38$ C or higher; *flammea*, -27 to $+38$ C. Both upper and lower limits were lower than for any other passerine species similarly studied. These limits were established using feed with a caloric content of 4.4 kcal/g. By substituting the higher caloric value of birch seeds (the major natural food) these estimated lower limits drop to -57 C for *hornemanni* and -51 C for

flammea. The lower limits for birds held under fluctuating temperatures and photoperiods, simulating actual periods of winter weather occurring at Fairbanks, Alaska, were probably closer to those for wild birds. These limits were for *hornemanni*, -44 C, and for *flammea*, -34 C. Again substituting the caloric value of birch seeds the respective values are -67 and -54 C.

The most important adaptations of the redpolls to the arctic winter, in comparison to non-arctic passerines, are:

1. Relatively higher rate and quantity of gross energy intake at low temperatures, owing in part to the possession of a crop-like esophageal diverticulum which is filled with "extra" food just prior to the onset of darkness.
2. Selection of high-calorie foods (primarily birch seeds) over foods containing fewer calories per unit weight.
3. The ability to increase digestive efficiency at extreme low temperatures.
4. Plumage with probable greater insulative value.
5. The ability to continue activities at very low light intensities.

Hornemanni is better adapted than *flammea* by being slightly more extreme in each of these adaptations (excepting diet selection) and, in addition, this species may not decrease its food intake during the autumn molting period to the degree that *flammea* does, thereby maintaining fat reserves for use during early, sudden cold periods in its more northern environment.

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